POPULATION STRUCTURE IN A SNAIL SPECIES FROM ISOLATED MALAYSIAN LIMESTONE HILLS, INFERRED FROM RIBOSOMAL DNA SEQUENCES

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ABSTRACT

We sequenced the first internal transcribed spacer (ITS-1) of the ribosomal DNA in nine populations of the vertiginid Gyliotrachela hungerfordiana, which lives on isolated (and threatened) limestone hills in the Malaysian peninsula. Current data suggest that the species is an obligate calcicole. The application of a tentative molecular clock suggests a Quaternary divergence for the G. hungerfordiana populations. A strong positive correlation between genetic and geographic distance was observed, which, combined with geological data, suggests that the hill populations may be interconnected by as yet unsampled populations.

Key words: internal transcribed spacer, ITS-1, Gastropoda, Pulmonata, Vertiginidae,

Gyliotrachela, gene flow, Southeast Asia.

INTRODUCTION

Land snails have proverbially poor abilities for dispersal (e.g., Cowie, 1984; Schilthuizen & Lombaerts, 1994), which causes them to show evolutionary patterns at much smaller spatial scales than many other organisms of similar size. As a result, strong geographic structuring of populations is common in snails (e.g., in Liguus; Hillis et al., 1987). Another consequence is endemism, which is seen, for example, in the Mediterranean clausiliid genus Albinaria, of which almost 30 species are endemic to the island of Crete, with distribution areas of sometimes only one kilometer across (Gittenberger, 1991; Welter-Schultes, 1998).

An impressive situation of high endemism and geographic structuring of land snails in a strongly fragmented habitat exists in peninsular Malaysia. Here, limestone is exposed in the form of "tower karst" and other karstifications, limited to about three hundred hills, scattered over the peninsula. These hills are often very small, the largest with a diameter of a few kilometers, but most measuring only a few hundred meters across. In spite of their small size, the hills are a prominent feature of the landscape, because they usually stand isolated, are riddled with caves and are bounded by precipitous cliffs.

For more than a century, malacologists have been interested in the rich malacofauna that the hills support (de Morgan, 1885). High numbers of species are found, and the morphologies of some Diplommatinidae foreshadow the bizarre and extravagant forms found in this group in Borneo (Vermeulen, 1993, 1994; Gittenberger, 1995). But especially fascinating is the staggering degree of endemism in these calcicolous snails. Tweedie (1961) gave an overview of six taxa containing many obligate calcicoles (Diplommatina, Opisthostoma, Vertiginidae, Discartemon. Oophana. and Sinoennea). He listed the presence of 106 species on 28 hills or hillclusters, of which 70 are endemic to only one locality. Some calcicolous species, however, are widespread and occur on almost all hills without a trace of morphological differentiation (e.g. Gyliotrachela hungerfordiana and some Alycaeus species).

Geologically, the hills form the exposed parts of a number of larger paleozoic limestone deposits, which are elsewhere overlain by non-calciferous alluvial deposits (Gale, 1986; Crowther, 1986). Some hills may thus have been connected in the past, while others have always been separate. Consequently, the hills form virtual "islands" for obligately calcicolous land snails, which they may reach by incidental dispersal. Alternatively, the pop-

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ulations on the hills may be relicts from a time when the hills were part of large continuous plateaus, which were subsequently fragmented.

In this paper, we examine a relatively widespread representative of the peninsular Malaysian hill malacofauna, using molecular and geological data, to answer the following questions: (1) what pattern of phylogeographic relationships exists among the populations of this widespread species, and (2) how has the population structure been shaped, that is, what are the relative influences of dispersal and habitat fragmentation over geological time?

By analyzing the variance in a noncoding nuclear DNA marker, we attempt to differentiate between various alternative population structures. In the case of ancient vicariance. we expect to find genetic distances that reflect the age of fragmentation of the limestone hills. while dispersal would result in genetic distances more or less related to geographic distance. Under the latter hypothesis (dispersal). indications of the type and frequency of dispersal may be gleaned from the degree of correlation between genetic and geographic distance; if dispersal is randomly oriented (i.e., corresponding to an island model of population structure; Wright, 1931), stochasticity would result in a poor fit, while dispersal occurring mainly among neighboring hills (i.e., corresponding to a stepping-stone model; Kimura, 1953) would be revealed by a strong correlation (Kimura & Weiss, 1964).

Sadly, there are other motives for working on this fauna. The hills of peninsular Malaysia are disappearing and becoming depauperate at an alarming rate. Forest clearing has destroyed the vegetation on some hills; and in the densely populated areas near lpoh and Kuantan, many hills are being removed by quarrying. The true rate of species loss can only be guessed at, but the extinction of at least one endemic snail species, *Opisthostoma sciaphilum*, from Bukit Panching, has been documented (Schilthuizen et al., unpubl.).

MATERIAL AND METHODS

Selection of Taxa

We selected the widespread and morphologically uniform vertiginid *Gyliotrachela hungerfordiana* for study (Fig. 1). The related

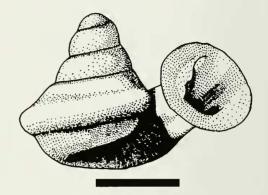


FIG. 1. Gyliotrachela hungerfordiana (von Möllendorff). Scale bar = 1 mm.

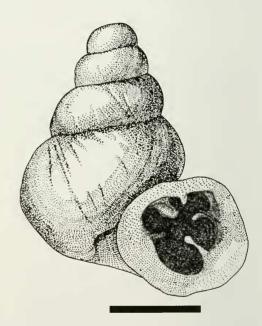


FIG. 2. *Gyliotrachela frequens* van Benthem Jutting. Scale bar = 1 mm.

species *G. frequens* (Fig. 2) was selected to serve as an outgroup in the phylogenetic analysis.

Collecting

In July 1997, the first author visited 22 limestone hills in the West-Malaysian states of Pahang, Kelantan, Perak and Perlis. Living snails were discovered by eye using two strategies: (a) close inspection of limestone rock faces,

either damp or dry, bare or covered in algae, mosses and lichens; and (b) sifting through damp and decaying leaf litter on limestone rocks or at the base of the limestone cliffs. All snails were put in 100% ethanol on the spot and kept at ambient temperatures until arrival in the laboratory for further processing. Identification of the material was carried out by the second author while the material remained in alcohol. Gvliotrachela hungerfordiana was collected from nine of the 22 localities (Fig. 3): loc. 5. State of Pahang: Gua Bama (ca. 10 km W of Kuala Lipis): loc. 8. State of Kelantan: Gua Musang, southern of the two hills that the road to Kuala Kerai passes between; loc. 9, State of Kelantan: rocks 59 km in the direction of Gua Musang, measured along the road from Kuala Krai; loc. 16, State of Perak: Bukit Tambun (ca. 6 km E of lpoh); loc. 22, State of Perak: hill directly east of Sungai Siput Utara hospital: loc. 23, State of Perlis: hill ca. 1 km S of Kangar: loc. 24. State of Perlis: 9 km along the road from Kangar to Kaki Bukit: loc. 25. State of Perlis: Gua Kelam at Kaki Bukit: loc. 26. State of Perlis, Timah Tasoh (ca. 16 km NE of Kangar). All samples were taken between 27.vi.1997 and 17.vii.1997. Gyliotrachela frequens was taken only from locality 8. Voucher specimens have been deposited in the collection of the National Museum of Natural History "Naturalis". Leiden.

Molecular Techniques

DNA was isolated from pools of between one and five complete snails with their shells, using either a phenol/chloroform extraction as described previously (Schilthuizen et al., 1998a) or a sucrose-based protocol (van Moorsel & van Nes, unpublished), which can be briefly summarized as follows. Snails were ground in 200 µl of sucrose-buffer (0.1 M Tris; 0.02 M NaCl: 0.2 M sucrose: 0.05 M EDTA) and centrifuged. The pellet was incubated at 65°C for 60 min in 200 μl SDS-buffer (0.02 M Tris; 0.01 M EDTA, 1.25% SDS), 15 ul of cold KAc was added, and the mixture was incubated on ice for 60 min and centrifuged. The DNA was precipitated from the supernatant by the addition of two volumes of 100% ethanol and incubation at -20°C for 30 min. The DNA was dried and treated with 200 ng of RNase. Full details can be obtained from M.S. on request. Homogenization was always done with a sterile, disposable plastic pestle. The DNA was dissolved in 50 µl of Tris-EDTA buffer (phenol protocol) or 30 µl of ddH2O (sucrose protocol) and stored at -20°C. The first internal transcribed spacer of the nuclear ribosomal DNA was amplified with the SuperTag enzyme (HT Biotechnology, Cambridge, England) as described previously (Schilthuizen et al., 1995) and isolated using the "freezesqueeze" technique (Tautz & Renz, 1983). Because PCR-amplification was at times too weak for direct sequencing, we resorted to cloning (PCR-based error is usually not a concern with this methodology; Schilthuizen et al., 1998b). After isolation, the fragments were ligated into Promega or Invitrogen T-tailed vectors, following the manufacturer's instructions. Colonies were screened for the presence of the correct insert by PCR. Plasmid DNA was isolated from the bacteria using QIAPrep spin columns (QIAGEN). One or two clones per sample were sequenced in both directions on an ABI automated sequencer.

Alignment

Before alignment, all chromatograms were checked and reading errors were corrected blindly where necessary (this never amounted to more than three corrections in a single sequence). Vector and primer sequences were removed. Sequences in the ingroup were sufficiently similar to allow manual alignment. Wherever alignment with the outgroup was ambiguous, missing data were introduced into the outgroup sequence.

Phylogenetic Analysis

Phylogenetic analyses of the data set were performed in PAUP3.1 (Swofford, 1993). Gaps were treated as missing data. Searches for the most parsimonious trees were carried out with the branch-and-bound option. Bootstrap replicates were carried out 100 times, using heuristic searches. In addition, Bremer (1988) support was determined. Kimura's 2-parameter genetic distances (Kimura, 1980) were calculated with the DNADIST program of the PHYLIP package (Felsenstein, 1995).

RESULTS

PCR-products ranged in length from 755 to 772 bp, including primers (52 bp), and the flanking regions of 18S (146 bp) and 5.8 S (87 bp). These lengths correspond well with other ITS-1 lengths reported in mollusks (Anderson

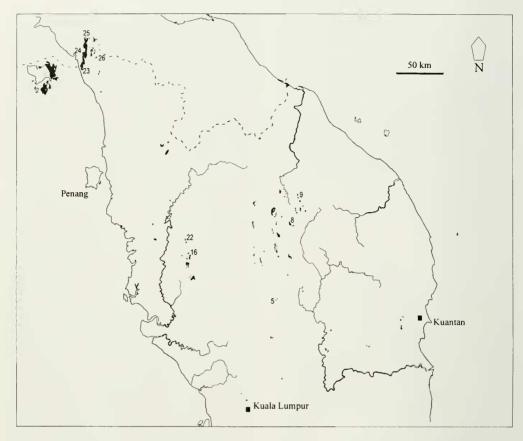


FIG. 3. A map of the northern part of Peninsular Malaysia, with the limestone hills drawn in black (modified after Gobbett, 1965). The numbers refer to localities where *Gyliotrachela hungerfordiana* and *G. frequens* were collected (see text for further details).

& Adlard, 1994; Schilthuizen et al., 1995; Armbruster et al., unpubl.).

We obtained sixteen sequences from G. hungerfordiana and one sequence for the outgroup, G. frequens (Appendix, Table 1). They have been deposited in GenBank under accession numbers AF118000-AF118016. Only small genetic distances were found among the G. hunderfordiana sequences, the largest being 0.048 between sequence a from locality 5 and sequence b from locality 23. A comparison between pairwise genetic distances and pairwise geographic distances between sequences revealed a strongly significant (p < 0.005) positive correlation (Fig. 4, Appendix, Table 2). The phylogenetic analysis produced 18 most parsimonious trees (length = 89 steps, RI = 0.95), which showed two

alternative topologies for three monophyletic groups of sequences, and otherwise only minor differences in topology within each of these three monophyletic groups (Figs. 5, 6). The fact that duplicate sequences from a single locality always formed monophyletic groups might justify the small sample sizes. Geographic structuring is apparent in the trees also, as these show monophyly for the sequences derived from populations in Perlis, Pahang + Kelantan, and Perak.

DISCUSSION

Unfortunately, it is difficult to estimate reliably from the molecular data the time since divergence. Unlike the situation for mitochon-

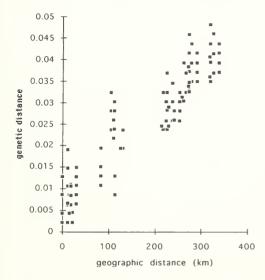


FIG. 4. The relationship between geographic distance and Kimura's 2-parameter distance for the sequences of *Gyliotrachela hungerfordiana*.

drial DNA, corroborated molecular clocks for the ITS regions are hardly available yet, and where they are, they differ by orders of magnitude among taxonomic groups. In the angiosperm families Cucurbitaceae and Winteraceae, substitution rates of 3.62×10^{-3} and 3.4×10^{-4} per site per million years (MY) were calculated, respectively (Jobst et al., 1998; Suh et al., 1993), while in Chlorophyta, a rate of $0.8 - 2.0 \times 10^{-2}$ was estimated (Bakker et al., 1995). In animals, rates of substitution in ITS appear to be somewhat higher. Schlötterer et al. (1994) give a figure of 1.2 × 10⁻² for *Drosophila*, and preliminary data for clausiliid land snails from Greek islands indicate a similar rate (van Moorsel, unpublished data).

Here, we will adopt a substitution rate of 1×10^{-2} per site per MY as a very rough molecular clock. Applying this rate to the average genetic distance between sequences on either side of the node basal to all *G. hungerfordiana* sequences in the trees, we obtained an estimated divergence time of 1.8 MYA for the populations of *G. hungerfordiana*. It should be stressed that, given the lack of agreement in the few calibrated molecular clocks available, not too much confidence should be placed on this date. However, it may be safe to assume a Late Tertiary or Quaternary origin for *G. hungerfordiana*.

Given the low degree of genetic divergence among the G. hungerfordiana populations, it seems unlikely that vicariance has played an important role: hills which have been studied geologically are thought to be older than Late Tertiary/Quaternary (Gale, 1986), However, in view of the uncertainty about the calibration of the ITS-1 molecular clock, this reasoning may be little meaningful. More importantly, geological data indicate that most of the hills from which the species was sampled have never been part of one continuous plateau (Paton. 1961). It is for this reason not likely that vicariance events have been important in its distribution pattern. Rather, the limestone hills on which it lives now must have been colonized after dispersal.

Several mechanisms for passive dispersal in small snails have been suggested, including wind and water mediated dispersal. In reference to Gyliotrachela and similar snails. Tweedie (1961) has suggested that flooding may be important in producing dispersal among hills that are situated close together. However, the drainage patterns in the peninsula preclude any long-range dispersal by this mechanism. Stagnant water may also provide means of dispersal, and geological data (Gale, 1986; Crowther, 1986) indicate that lacustrine conditions have prevailed around several limestone hills in the past. But here, too, dispersal would be across very small distances. Another possibility is wind-dispersal. Kirchner et al. (1997) demonstrate how Truncatellina, a vertiginid very similar in size to G. hungerfordiana, could be blown over distances of several kilometers during storms.

Some additional characteristics of dispersal may be gleaned from Figure 4, which suggests a linear relationship between geographic and genetic distance. If dispersal from one hill to another were infrequent and undirected (i.e., a population structure corresponding to Wright's [1931] island model, where all possible pairs of subpopulations are equally likely to exchange migrants), such a clear relation would not be expected. The fact that genetic distance is reliably predicted ($r^2 = 0.77$) by geographic distance, suggests that a structured network of dispersal connects the hills. This corresponds to a stepping-stone model (Kimura, 1953). Under such a model, genetic similarities drop steeply with increasing numbers of intervening populations (Kimura & Weiss, 1964). The fact that we observe a strong relationship with geographic distance, suggests that the hill popu-

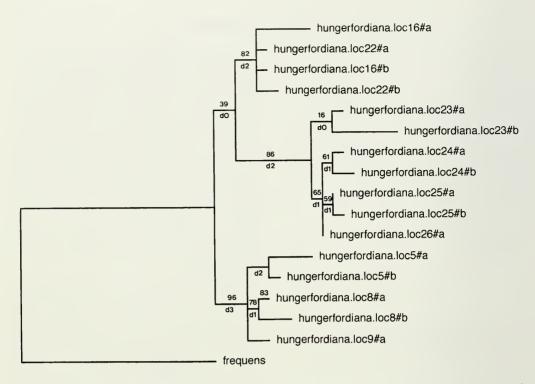


FIG. 5. A representative most parsimonious tree of the *Gyliotrachela* sequences. Bootstrap percentages and decay indices have been indicated on the branches.

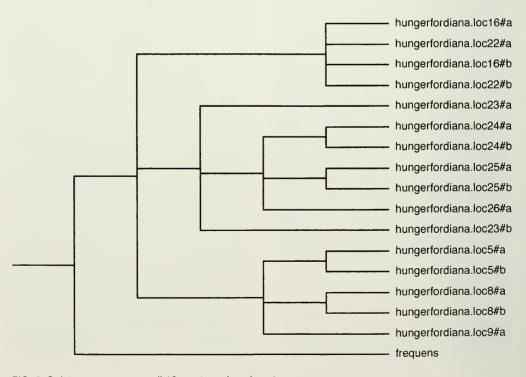


FIG. 6. Strict consensus over all 18 most parsimonious trees.

lations cannot represent directly adjacent populations in a two-dimensional stepping-stone lattice. Rather, to obtain this result, it is necessary to postulate unsampled populations in between. Unfortunately, the population genetics of ribosomal DNA are as vet far from clear (Hillis et al., 1991; Rich et al., 1997), which makes a quantitative analysis of dispersal parameters and spatial details of the population structure impossible. Therefore, it is not possible to tell whether the hills that separate our sample sites (e.g., the six or more hills between sites 8 and 9) will suffice as additional stepping stones. This might be tested, for instance, by exhaustively sampling the hills in a given subregion.

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APPENDIX

TABLE 1. Aligned sequences for *Gyliotrachela hungerfordiana* and *G. frequens*. The 5' end of the 18S region is at position 146, the 3' end of the 5.8S region is at position 694.

CGGTCTGGTG CGCAAGTGCC	GGATTGGTCT GGATTGGTCT GGATTGGTCT GGATTGGTCT GGATTGGTCT GGATTGGTCT	TGAGGGCCTC TGAGGGCCTC TGAGGGCCTC	AGCGGTTCAG AGCGGTTCAG	hungerfordiana.loc5#a hungerfordiana.loc5#b hungerfordiana.loc8#a
CGGTCTGGTG CGCAAGTGCC	GGATTGGTCT GGATTGGTCT GGATTGGTCT GGATTGGTCT GGATTGGTCT GGATTGGTCT	TGAGGGCCTC TGAGGGCCTC TGAGGGCCTC	AGCGGTTCAG AGCGGTTCAG	hungerfordiana.loc5#b
CGGTCTGGTG CGCAAGTGCC	GGATTGGTCT GGATTGGTCT GGATTGGTCT GGATTGGTCT	TGAGGGCCTC TGAGGGCCTC	AGCGGTTCAG	
CGGTCTGGTG CGCAAGTGCC	GGATTGGTCT GGATTGGTCT GGATTGGTCT	TGAGGGCCTC		iunger rordrana. roco#a
CGGTCTGGTG CGCAAGTGCC CGGTCTGGTG CGCAAGTGCC CGGTCTGGTG CGCAAGTGCC CGGTCTGGTG CGCAAGTGCC CGGTCTGGTG CGCAAGTGCC CGGTCTGGTG CGCAAGTGCC	$\begin{array}{c} {\sf GGATTGGTCT} \\ {\sf GGATTGGTCT} \\ {\sf GGATTGGTCT} \end{array}$	TGAGGGCCTC	TAGCGGTTCAG	
CGGTCTGGTG CGCAAGTGCC CGGTCTGGTG CGCAAGTGCC CGGTCTGGTG CGCAAGTGCC CGGTCTGGTG CGCAAGTGCC CGGTCTGGTG CGCAAGTGCC	$\begin{array}{c} {\tt GGATTGGTCT} \\ {\tt GGATTGGTCT} \end{array}$			ungerfordiana.loc8#b
CGGTCTGGTG CGCAAGTGC CGGTCTGGTG CGCAAGTGC CGGTCTGGTG CGCAAGTGC CGGTCTGGTG CGCAAGTGC CGGTCTGGTG CGCAAGTGC	${\tt GGATTGGTCT}$		AGCGGTTCAG	ungerfordiana.loc9#a
CGGTCTGGTG CGCAAGTGC CGGTCTGGTG CGCAAGTGC CGGTCTGGTG CGCAAGTGC CGGTCTGGTG CGCAAGTGC		TGAGGGCCTC	AGCGGTTCAG	ungerfordiana.loc16#a
CGGTCTGGTG CGCAAGTGC CGGTCTGGTG CGCAAGTGC CGGTCTGGTG CGCAAGTGC CGGTCTGGTG CGCAAGTGC		TGAGGGCCTC	AGCGGTTCAG	ungerfordiana.loc16#b
CGGTCTGGTG CGCAAGTGC CGGTCTGGTG CGCAAGTGC CGGTCTGGTG CGCAAGTGC	GGATTGGTCT	TGAGGGCCTC	AGCGGTTCAG	ungerfordiana.loc22#a
CGGTCTGGTG CGCAAGTGC			1	ungerfordiana.loc22#b
CGGTCTGGTG CGCAAGTGC				
				ungerfordiana.loc23#a
CGGTCTGGTG CGCAAGTGC				ungerfordiana.loc23#b
	GGATTGGTCT	TGAGGGCCTC	AGCGGCTCAG	ungerfordiana.loc24#a
CGGTCTGGTG CGCAAGTGC	GGATTGGTCT	TGAGGGCCTC	AGCGGTTCAG	ungerfordiana.loc24#b
CGGTCTGGTG CGCAAGTGC	GGATTGGTCT	TGAGGGCCTC	AGCGGTTCAG	ungerfordiana.loc25#a
CGGTCTGGTG CGCAAGTGC				ungerfordiana.loc25#b
CGGTCTGGTG CGCAAGTGC				ungerfordiana.loc26#a
CGGTCTGGTG CGCAAGTGC	GGATTGGTCT		AGCGGTTCAG	requens
90 1	80	7	60	
CGATCGCTTG GAGAAAGTA	AGCTCGAACT	GCCGAGAAG	GGCACCGCTG	ungerfordiana.loc5#a
CGATCGCTTG GAGAAAGTA				ungerfordiana.loc5#b
CGATCGCTTG GAGAAAGTA				ungerfordiana.loc8#a
CGATCGCTTG GAGAAAGTA				ungerfordiana.loc8#b
CGATCGCTTG GAGAAAGTA				ungerfordiana.loc9#a
CGATCGCTTG GAGAAAGTA	AGCTCGAACT	GCCGAGAAGA	GGCGCCGCTG	ingerfordiana.loc16#a
CGATCGCTTG GAGAAAGTA				ingerfordiana.loc16#b
CGATCGCTTG GAGAAAGTA			1	ingerfordiana.loc22#a
CGATCGCTTG GAGAAAGTA				ingerfordiana.loc22#b
CGATCGCTTG GAGAAAGTA				ingerfordiana.loc23#a
CGATCGCTTG GAGAAAGTA				ungerfordiana.loc23#b
CGATCGCTTG GAGAAAGTA	AGCTCGAACT	GCCGAGAAG?	GGCACCGCTG	ungerfordiana.loc24#a
CGATCGCTTG GAGAAAGTA	AGCTCGAACT	GCCGAGAAGA	GGCACCGCTG	ungerfordiana.loc24#b
CGATCGCTTG GAGAAAGTA	AGCTCGAACT	GCCGAGAAGA	GGCACCGCTG	ungerfordiana.loc25#a
CGATCGCTTG GAGAAAGTA				ungerfordiana.loc25#b
CGATCGCTTG GAGAAAGTA				
				ungerfordiana.loc26#a
CGATCGCTTG GAGAAAGTA	AGCCCGAACT	GCCGAGAAGA	GGCACCGCTG	requens
140 1	130	12	110	
TGCGGAAGGA TCATTAACG	TAGGTGAACC	AAGGTTTCCC	AAGTCGTAAC	ingerfordiana.loc5#a
TGCGGAAGGA TCATTAACG	TAGGTGAACC	AAGGTTTCCC	AAGTCGTAAC	ungerfordiana.loc5#b
TGCGGAAGGA TCATTAACG				ingerfordiana.loc8#a
TGCGGAAGGA TCATTAACG			AAGTCGTAAC	ingerfordiana.loc8#b
TGCGGAAGGA TCATTAACG			AAGTCGTAAC	ingerfordiana.loc9#a
TGCGGAAGGA TCATTATCG			AAGTCGTAAC	ingerfordiana.loc16#a
TGCGGAAGGA TCATTATCG	TAGGTGAACC	AAGGTTTCCC	AAGTCGTAAC	ngerfordiana.loc16#b
TGCGGAAGGA TCATTATCG	TAGGTGAACC	AAGGTTTCCC	AAGTCGTAAC	ingerfordiana.loc22#a
TGCGGAAGGA TCATTATCG			AAGTCGTAAC	ingerfordiana.loc22#b
TGCGGAAGGA TCATTATCG			AAGTCGTAAC	ingerfordiana.loc23#a
TGCGGAAGGA TCATTATCG				
TGCGGAAGGA TCATTATCG				
TGCGGAAGGA TCATTATCG			AAGTCGTAAC	
TGCGGAAGGA TCATTATCGG	TAGGTGAACC	AAGGTTTCCC	AAGTCGTAAC	ingerfordiana.loc25#a
TGCGGAAGGA TCATTATCG				
TGCGGAAGGA TCATTATCG				
	TAGGTGAACC TAGGTGAACC TAGGTGAACC TAGGTGAACC TAGGTGAACC	AAGGTTTCCC AAGGTTTCCC AAGGTTTCCC AAGGTTTCCC	AAGTCGTAAC AAGTCGTAAC AAGTCGTAAC	hungerfordiana.loc23#b hungerfordiana.loc24#b hungerfordiana.loc25#a hungerfordiana.loc25#b hungerfordiana.loc25#b hungerfordiana.loc26#a frequens

TABLE 1. Continued.

TABLE 1. Continued.					
	160	170	180	190	200
hunganfanding last#s	ma ma a m	- CAMON			
hungerfordiana.loc5#a			GGCTGCAGCG		
hungerfordiana.loc5#b			GGCAGCAGCG		
hungerfordiana.loc8#a	TATAAT	CATCA	GGCAGCAGCG	GGGCGCGCAG	CGGCTTATGA
hungerfordiana.loc8#b	TATAAT	CATCA	GGCAGCAGCG	GGGCGCGCAG	CGGCTTATGA
hungerfordiana.loc9#a			GGCAGCAGCG		
hungerfordiana.loc16#a			GGCAGCAGCG		
hungerfordiana.loc16#b			GGCAGCAGCG		
hungerfordiana.loc22#a			GGCAGCAGCG		
hungerfordiana.loc22#b			GGCATCAGCG		
hungerfordiana.loc23#a	TATAAT	CATCA	GGCAGCAGCG	GGGCACGCAG	CGGCTTGTGA
hungerfordiana.loc23#b	TATAAT	CATCA	GGCAGCAGCG	GGGCGCGCAG	CGGCTTGTGA
hungerfordiana.loc24#a	TACAAT	CATCA	GGCAGCAGCG	GGGCGCGCAG	CGGCTTGTGA
hungerfordiana.loc24#b	TACAAT	CATCA	GGCAGCAGCG	GGGCGCGCAG	CGGCTTGTGA
hungerfordiana.loc25#a			GGCAGCAGCG		
hungerfordiana.loc25#b			GGCAGCAGCG		
hungerfordiana.loc26#a			GGCAGC		
frequens			GGC		
	210	220	230	240	250
hungerfordiana.loc5#a	TGAAATTA	TGCTGAT	TGAACGTCTG	TC	
hungerfordiana.loc5#b		TGCTGAT		TC	
hungerfordiana.loc8#a		TGCTGAT		TC	
hungerfordiana.loc8#b		TGCTGGT		TC	
hungerfordiana.loc9#a		TGCTGAT		TC	
hungerfordiana.loc16#a		TGCTGAT		TC	
hungerfordiana.loc16#b	,	TGCTGAT		TC	
hungerfordiana.loc22#a	ſ	TGCTGAT		TC	
hungerfordiana.loc22#b			TGAACGTCTG		
hungerfordiana.loc23#a		TGCTGAT		TC	
hungerfordiana.loc23#b		TGCTGAT		TC	
hungerfordiana.loc24#a			TGAACGCCTG		
1 2					
hungerfordiana.loc24#b			TGAACGCCTG		
hungerfordiana.loc25#a			TGAACGCCTG		
hungerfordiana.loc25#b			TGAACGCCTG		
hungerfordiana.loc26#a			TGAACGCCTG		
frequens	TGTATAGA	TAATGCTGAT	GGAACGTGTC	TEGTETEGTE	TCGTCTCGTC
	260	270	280	290	300
hungerfordiana.loc5#a	TCCCGTT	GCCGATCGGG	GACCGCAAGA	AGCGCCGCCC	CGGTCGGTTG
hungerfordiana.loc5#b			GACCGCAAGA		CGGTCGGTTG
hungerfordiana.loc8#a			GACCGCAAGA		
hungerfordiana.loc8#b			GACCGCAAGA		CGGTCGGTCG
hungerfordiana.loc9#a			GACCGCAAGA		CGGTCGGTTG
hungerfordiana.loc16#a			GACCGCAAGA		CGGTCGGTTG
hungerfordiana.loc16#b	1		GACCGCAAGA		CGGTCGGTTG
hungerfordiana.loc22#a					CGGTCGGTTG
hungerfordiana.10c22#a			GACCGCGAGA GACCGCAAGA		
	1				
hungerfordiana.loc23#a	1		GACCGCAAGA		CGGTCGGTTG
hungerfordiana.loc23#b			GACCGCAAGA		CGGTCGGTTG
hungerfordiana.loc24#a			GACCGCAAGA		CGGTCGGTTG
hungerfordiana.loc24#b			GACCGCAAGA		
hungerfordiana.loc25#a			GACCGCAAGA		
hungerfordiana.loc25#b			GACCGCAAGG		
hungerfordiana.loc26#a					
frequens	TCGTCTCATT	GCCGATCGGG	GACCGCAAGA	AGCGCCGCCC	CGGTCGGTTG

TABLE 1. Continued.

TABLE 1. Continued.					
	310	320	330	340	350
hungerfordiana.loc5#a	ACCGCTCCCC	TGTTTCGGGG	TACCTAGTCT	TATCTCGCAC	TCAATACGGC
hungerfordiana.loc5#b	ACCGCTCCCC	TGTTTCGGGG	TACCTAGTCT	TATCTCGCAC	TCAATACGGC
hungerfordiana.loc8#a	ACCGCTCCCC	TGTTTCGGGG	TACCTAGTCT	TATCTCGCAC	TCAATACGGC
hungerfordiana.loc8#b	ACCGCTCCCC	TGTTTCGGGG	TACCTAGTCT	TATCTCGCAC	TCAATACGGC
hungerfordiana.loc9#a	ACCGCTCCCC	TGTTTCGGGG	TACCTAGTCT	TATCTCGCAC	TCAATACGGC
hungerfordiana.loc16#a	ACCGCTCCCC	TGTTTCGGGG	TACCTAGTCT	TATCTCGCAC	TCAATACGGC
hungerfordiana.loc16#b	ACCGCTCCCC	TGTTTCGGGG	TACCTAGTCT	TATCTCGCAC	TCAATACGGC
hungerfordiana.loc22#a	ACCGCTCCCC	TGTTTCGGGG	TACCTAGTCT	TATCTCGCAC	TCAATACGGC
hungerfordiana.loc22#b	ACCGCTCCCC	TGTTTCGGGG	TACCTAGTCT	TATCTCGCAC	TCAATACGGC
hungerfordiana.loc23#a	ACCGCTCCCC	TGTTTCGGGG	TACCTAGTCT	TATCTCGCAC	TCAATACGGC
hungerfordiana.loc23#b	ACCGCTCCCC	TGTTTCGGGG	TACCTAGTCT		TCAATACGGC
hungerfordiana.loc24#a	ACCGCTCCCC	TGTTTCGGGG	TACCTAGTCT	TATCTCGCAC	TCAATACGGC
hungerfordiana.loc24#b	ACCGCTCCCC	TGTTTCGGGG	TACCTAGTCT	TATCTCGCAC	TCAATACGGC
hungerfordiana.loc25#a	ACCGCTCCCC		TACCTAGTCT		TCAATACGGC
hungerfordiana.loc25#b hungerfordiana.loc26#a	ACCGCTCCCC		TACCTAGTCT TACCTAGTCT	TATCTCGCAC TATCTCGCAC	TCAATACGGC TCAATACGGC
frequens			TACCTAGTCT		
rrequeits	ACCGCTCCCC	1611106666	TACCTAGICT	CGTCTCGCAC	
	360	370	380	390) 400
hungerfordiana.loc5#a	CCACGGTGAC	GGCAAGAGCT	TTCAGCTCGC	CGGGTCGTCA	GGTCTAAGGA
hungerfordiana.loc5#b	CCACGGTGAC	GGCAAGAGCT	TTCAGCTCGC	CGGGTCGTCA	GGTCTAAGGA
hungerfordiana.loc8#a	CCACGGTGAC	GGCAAGAGCT	TTCAGCTCGC	CGGGTCGTCA	GGTCTAAGGA
hungerfordiana.loc8#b	CCACGGTGAC	GGCAAGAGCT		${\tt CGGGTCGTCA}$	
hungerfordiana.loc9#a	CCACGGTGAC		TTCAGCTCGC		
hungerfordiana.loc16#a			TTCAGCTCGC		
hungerfordiana.loc16#b	CCACGGTGAC	GGCAAGAGCT		CGGGTCGTCA	
hungerfordiana.loc22#a	CCACGGTGAC			CGGGTCGTCA	
hungerfordiana.loc22#b			TTCAGCTCGC		
hungerfordiana.loc23#a			CTCAGCTCGC		
hungerfordiana.loc23#b	1		TTCAGCTCGC		
hungerfordiana.loc24#a	1		TTCAGCTCGC		
hungerfordiana.loc24#b hungerfordiana.loc25#a		GGCAAGAGCT GGCAAGAGCT		CGGGTCGTCA	
hungerfordiana.10025#a	1 -	GGCAAGAGCT		CGGGTCGTCA	
hungerfordiana.loc26#a			TTCAGCTCGC		
frequens			CTCAGCTCGC		
ITEGUEIIS					
	410	420	430	440	450
hungerfordiana.loc5#a			TGAGCGGCGC		
hungerfordiana.loc5#b	I .		TGAGCGGCGC		
hungerfordiana.loc8#a			TGAGCGGCGC		
hungerfordiana.loc8#b			TGAGCGGCGC		
hungerfordiana.loc9#a	GCGCTGCTCT		TGAGCGGCGC		
hungerfordiana.loc16#a	GCGCTGCTCC	GACTGCTCTG		CGCCCCGGTG	
hungerfordiana.loc16#b	L .	GATTGCTCTG		CGCCCCGGTG	
hungerfordiana.loc22#a	GCGCTGCTCC	GATTGCTCTG		CGCCCCGGTG	
hungerfordiana.loc22#b hungerfordiana.loc23#a	GCGCTGCTCC	GATTGCTCTG		CGCCCCGGTG	
hungerfordiana.loc23#a	GCGCTGCTCT	GATTGCCCTG		CGCCCCGGTG	
hungerfordiana.10023#b		GATTGCTCTG		CGCCCCGGTG	
hungerfordiana.loc24#a	1		TGAGCGGCGC		
hungerfordiana.loc25#a			TGAGCGGCGC		
hungerfordiana.loc25#b	GCGCTGCTCT	GATTGCTCTG	TGAGCGGCGC	CGCCCCGGTG	ATTG-TGTGG
hungerfordiana.loc26#a	GCGCTGCTCT	GATTGCTCTG	TGAGCGGCGC	CGCCCCGGTG	ATTG-TGTGG
frequens	GCGCCGCTCT	GACTGCTCTA	TGAGCGGCGC	CGCCCCGGTA	GTTGGTGTGG

TABLE 1. Continued.

hungerfordiana.loc5#a hungerfordiana.loc8#b hungerfordiana.loc8#b hungerfordiana.loc8#b hungerfordiana.loc8#b hungerfordiana.loc8#b hungerfordiana.loc8#b hungerfordiana.loc9#a hungerfordiana.loc16#a hungerfordiana.loc16#b hungerfordiana.loc2#b hungerfordiana.loc6#a hungerfordiana.loc6#a hungerfordiana.loc6#b hungerfordiana.loc6#	TABLE 1. Continued.					
hungerfordiana.locs#b		460	470) 480	490	500
hungerfordiana.locs#b	6 1: 5//	l l				
hungerfordiana.loc8#b harATGGAG G		-ATAATGGAG	G	GTACCTG	TGCGCTCGAC	CCGCT-CTGC
AURAPTOGAG G		-ATAATGGAG	G	GTACCTG	TGCGCTCGAC	CCGCT-CTGC
hungerfordiana.loci6#a hungerfordiana.loci6#b hungerfordiana.loci6#b hungerfordiana.loci2#b hungerfordiana.loci4#b hungerfordiana.loci4#a						
hungerfordiana.loc16#a hungerfordiana.loc2#b		-ATAATGGAG	G	GTACCTG	TGCGCTCGAC	CCGCT-CTGC
hungerfordiana.loc22#b hungerfordiana.loc22#b hungerfordiana.loc22#b hungerfordiana.loc23#b hungerfordiana.loc23#b hungerfordiana.loc23#b hungerfordiana.loc24#b hungerfordiana.loc24#b hungerfordiana.loc24#b hungerfordiana.loc24#b hungerfordiana.loc24#b hungerfordiana.loc25#b hungerfordiana.loc25#b hungerfordiana.loc25#b hungerfordiana.loc25#b hungerfordiana.loc25#b hungerfordiana.loc25#b hungerfordiana.loc25#b hungerfordiana.loc26#a **TRACGGAG G		-ATAATGGAG	G	GTACCTG	TGCGCTCGAC	CCGCT-CTGC
AUMGERFORDIANA.10c22#b ATRANGGAG G		GATAATGGAG	G	GTACCTG	TGCGCTCGAC	CCGCT-CTGC
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ATAACGGAG G						
hungerfordiana.loc25#b hungerfordiana.loc25#b hungerfordiana.loc25#b hungerfordiana.loc25#b hungerfordiana.loc26#a **Faguens** TCGCCGGATC CGGTCCGAC CCGCTCCTGC **Faguens** TCGCCGATC CGGTCCGAC CCGCTCCTGC **ATAACGGAG G						
hungerfordiana.loc25#a ATRACGGAG GGTACCTG TGCGCTGGAC CCGCTGCTGAC CGGTGCTGAC CGGTGCGAC AGGCCGGAC CGGGTGCGAT AGCTCCTGCG GTGCAAACGC AGGCCGGAC CGGGTGCGAT AGCTCCTGCG GTGCAAACGC AGGCCGGAC CGGGTGCGAT AGCTCCTGCG GTGCAAACGC AGGCCGGAC AGGGGTC CGGGTGCGAT AGCTCCTGCG GTGCAAACGC AGGCCGGAC AGGCGGGTC CGGGTGCGAA AGCTCTGCG GTGCAAACGC AGGCCGGAC AGGCCGGAC AGGCCGGAC AGCTCCTGCG GTGCAAACGC AGGCCGGAC AGGCCGA						
AUNGERFORDIANA.10c25#b Lungerfordiana.10c5#a hungerfordiana.10c5#a hungerfordiana.10c28#a hungerfordiana.10c28#b Lungerfordiana.10c28#b Lungerfordiana.10c8#b Lungerfordiana.10c28#b Lungerfordi		-ATGACGGAG	G	GTACCTG	TGCGCTCGAC	CCGCTGCTGC
### ATTACAGGAG G						
ATCAAGGAG GCAAGGCCGG AGGGTACCTG TGCGCTCGAC CG-CT-CTGC S10						
Silo		-ATAACGGAG	CCAACCCCCC	ACCOMACCING	TGCGCTCGAC	CCGCTGCTGC
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hungerfordiana.locs#b hungerfordiana.loc2#b hungerfordiana.loc2#a hungerfordiana.loc2#b		510	520	530	540	550
hungerfordiana.locs#b hungerfordiana.loc2#b hungerfordiana.loc2#a hungerfordiana.loc2#b	hungerfordiana.loc5#a	TCGGCGGATC	CGGGTGCGAT	AGCTCCTGCG	GTGCAAACGC	AGGCCGCGA?
hungerfordiana.loe8#a hungerfordiana.loe9#a hungerfordiana.loe9#a hungerfordiana.loe16#a hungerfordiana.loe16#a hungerfordiana.loe22#b hungerfordiana.loe22#b hungerfordiana.loe22#b hungerfordiana.loe22#b hungerfordiana.loe22#b hungerfordiana.loe22#b hungerfordiana.loe22#b hungerfordiana.loe22#b hungerfordiana.loe24#a hungerfordiana.loe24#b hungerfordiana.loe24#b hungerfordiana.loe25#a hungerfordiana.loe25#a hungerfordiana.loe25#a hungerfordiana.loe26#a Frequens TCGGCGGGTT GGGTGCGAT GGGTGCGAT AGCTCCTGCG GTGCAAACGC AGGCCGCGAT AGCTCTGCG GTGCAAACGC AGGCCGCGAT AGCTCTGCG GTGCAAACGC AGGCCGCGAT AGCTCTGCG GTGCAAACGC AGGCCGCGAT AGCTCTGCG GTGCAAACGC AGGCCGCGAT AGCTCCTGCG GTGCAAACGC AGGCCGCGAT CGGGTGCGAG AGCTCCTGCG GTGCAAACGC AGGCCGCGCCAT CGGGTGCGAG AGCTCCTGCG GTGCAAACGC AGGCCGCGAT CGGGTGCGAG AGCTCCTGCG GTGCAAACGC AGCCCGCCGCTCC GGGTGCGAG AGCTCCTGCG GTGCAAACGC AGCCCGCTCC GGGTGCGAG AGCTCCTGCG GTGCAAACCC AGCCCGCTCC GGGCGCCCAT CGGGTGCGAG AGCTCCTGCG GTGCAAACCC AGCCCGCTCC CGGCGCCCAT CGGGGGTC CGGGCCCAT ATGCT CGAGCA?ACC CGCCCGCTCC CGCCGCTCC CGAGCA?ACC CGCCCGCTCC CGCCGCTCC CGCCGCTCC CGGCCCCAT CG						
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	rrequens	GCTTAAAGA?	GTCGGCC-AT	GCTCGCGGCT	-GACCC-GCC	CGCCCT

TABLE 1. Continued.

TABLE 1. Continued.	(1)	(2)	636	(4)	(50
	610	620	630	640	650
hungerfordiana.loc5#a	GTCTTCCT	TATTT-AATT	TGTTACGCTT	GGTGGCTCGT	CTGTCTTATT
hungerfordiana.loc5#b	GTCTTCCT	TATTT-AATT	TGTTACGCTT	GGTGGCTCGT	CTGTCTTATT
hungerfordiana.loc8#a	GTCTTCCT	TATTT-AATT	TGTTACGCTT	GGTGGCTCGT	CTGTCTTATT
hungerfordiana.loc8#b	GTCTTCCT	TATTT-AATT	TGTTACGCTT	GGTGGCTCGT	CTGTCTTATT
hungerfordiana.loc9#a	GTCTTCCT	TATTT-AATT	TGTTACGCTT	GGTGGCTCGT	CTGTCTTATT
hungerfordiana.loc16#a	GTCTTCCT	TATTT-AATT	TGTTACGCTT	GGTGGCTTGT	CTGTCTTATT
hungerfordiana.loc16#b	GTCTTCCT	TATTT-AATT	TGTTACGCTT	GGTGGCTCGT	CTGTCTTATT
hungerfordiana.loc22#a			TGTTACGCTT		
hungerfordiana.loc22#b		TATTT-AATT		GGTGGCTCGT	
hungerfordiana.loc23#a		TATTT-AATT		GCTGGCTCGT	
hungerfordiana.loc23#b		CATTT-AATT		GCTGGCTCGT	
hungerfordiana.loc24#a		TATTT-AATT		GCTGGCTCGT	
hungerfordiana.loc24#b		TATTT-AATT	TGTTACGCTT		
hungerfordiana.loc25#a			TGTTACGCTT		
hungerfordiana.loc25#b			TGTTACGCTT		
hungerfordiana.loc26#a		TATTT-AATT		GCTGGCTCGT	
frequens	GTC-TCCTCT	CATTTTATTT	TGTTACGCT-		-TGTCCGAT-
	660	670	680	690	700
hungorfordissa last#-	mcmc y cmm y c	CCAAAAA		A A C A COURT	CTCCTACA AC
hungerfordiana.loc5#a			C		
hungerfordiana.loc5#b			C		
hungerfordiana.loc8#a			C		
hungerfordiana.loc8#b hungerfordiana.loc9#a			C		
hungerfordiana.loc9#a			C		
nungerfordiana.10016#a nungerfordiana.10016#b			C		GTCGTACAAC
nungerfordiana.loc22#a			C		
nungerfordiana.loc22#a			C		
nungerfordiana.loc22#b			AAAACAAA-C		GTCGTACAAC
nungerfordiana.loc23#b			AAAAC?AAAC		
nungerfordiana.loc24#a			AAAAC		
hungerfordiana.loc24#b			AAAC		
hungerfordiana.loc25#a			AC		GTCGTACAAC
hungerfordiana.loc25#b			AC		
hungerfordiana.loc26#a			-AAACAAAAC		
frequens			AAAACAAAA-		
220440110					
	710	720	730	74(750
hungerfordiana.loc5#a			GCTCGTGCGT		
hungerfordiana.loc5#b			GCTCGTGCGT		
nungerfordiana.loc8#a	1		GCTCGTGCGT		
nungerfordiana.loc8#b			GCTCGTGCGT		
nungerfordiana.loc9#a			GCTCGTGCGT		
nungerfordiana.loc16#a			GCTCGTGCGT		
nungerfordiana.loc16#b			GCTCGTGCGT		
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nungerfordiana.loc25#b			GCTCGTGCGT		
hungerfordiana.loc26#a					
frequens .	TTTGAGCGGT	GGATCACTCG	GCTCGTGCGT	CGATGAAGAG	CGCAGCCAGC
		-			

TABLE 1. Continued.

	760	770	780	790	800
hungerfordiana.loc5#a	TGCGTGAATT	AATGTGAATT	GCAGAACACA		
hungerfordiana.loc5#b	TGCGTGAATT	AATGTGAATT	GCAGAACACA		
hungerfordiana.loc8#a	TGCGTGAATT	AATGTGAATT	GCAGAACACA		
hungerfordiana.loc8#b	TGCGTGAATT	AATGTGAATT	GCAGAACACA		
hungerfordiana.loc9#a	TGCGTGAATT	AATGTGAATT	GCAGAACACA		
hungerfordiana.loc16#a	TACGTGAATT	AATGTGAATT	GCAGAACACA		
hungerfordiana.loc16#b		AATGTGAATT			
hungerfordiana.loc22#a		AATGTGAATT			
		AATGTGAATT			
F9		AATGTGAATT			
hungerfordiana.loc23#b		?????????			
hungerfordiana.loc24#a		AATGTGAATT			
hungerfordiana.loc24#b		AATGTGAATT			
hungerfordiana.loc25#a	TGCGTGAATT	AATGTGAATT	GCAGAACACA		
hungerfordiana.loc25#b		AATGTGAATT			
hungerfordiana.loc26#a		AATGTGAATT			
frequens	TGCGTGAATT	AATGTGAATT	GCAGAACACA		

TABLE 2. Pairwise Kimura's 2-parameter distances among the *G. hungerfordiana* sequences.

hungerfordiana.loc5#a	0.0000															
hungerfordiana.loc5#b	0.0085	0.0000														
hungerfordiana.loc8#a	0.0129	0.0107	0.0000													
hungerfordiana.loc8#b	0.0193	0.0150	0.0085	0.0000												
hungerfordiana.loc9#a	0.0128	0.0085	0.0064	0.0107	0.0000											
hungerfordiana.loc16#a	0.0324	0.0280	0.0259	0.0302	0.0236	0.0000										
hungerfordiana.loc16#b	0.0280	0.0236	0.0215	0.0258	0.0193	0.0085	0.0000									
hungerfordiana.loc22#a	0.0280	0.0236	0.0215	0.0258	0.0193	0.0085	0.0042	0.0000								
hungerfordiana.loc22#b	0.0281	0.0237	0.0216	0.0259	0.0193	0.0085	0.0042	0.0042	0.0000							
hungerfordiana.loc23#a	0.0394	0.0349	0.0328	0.0372	0.0304	0.0282	0.0238	0.0238	0.0238	0.0000						
hungerfordiana.loc23#b	0.0481	0.0436	0.0414	0.0458	0.0391	0.0368	0.0324	0.0324	0.0324	0.0126	0.0000					
hungerfordiana.loc24#a																
hungerfordiana.loc24#b	0.0459	0.0413	0.0392	0.0436	0.0369	0.0345	0.0302	0.0302	0.0302	0.0105	0.0190	0.0042	0.0000			
hungerfordiana.loc25#a	0.0415	0.0370	0.0348	0.0392	0.0325	0.0302	0.0258	0.0258	0.0259	0.0064	0.0127	0.0042	0.0084	0.0000		
hungerfordiana.loc25#b	0.0437	0.0392	0.0370	0.0414	0.0347	0.0324	0.0280	0.0280	0.0280	0.0085	0.0148	0.0063	0.0105	0.0021	0.0000	
hungerfordiana.loc26#a	0.0405	0.0359	0.0337	0.0382	0.0313	0.0289	0.0244	0.0244	0.0244	0.0043	0.0108	0.0022	0.0065	0.0022	0.0044	0.0000